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São Tomé Island Endemic Treefrogs (*Hyperolius* spp.) and Land-Use Intensification: A Tale of Hope and Caution

Lena Strauß[1], Ricardo Faustino de Lima[2,3], Frank Riesbeck[4], and Mark-Oliver Rödel[1]

Abstract

Forest degradation is a major driver of the global biodiversity declines. However, responses to forest degradation vary greatly between taxa and are predominantly understudied. This study investigates the effects of land-use change on the endemic amphibian fauna of São Tomé Island (Central Africa), where a fast-growing human population increases pressure on forest resources. We sampled acoustic data on reed frog (*Hyperolius* spp.) abundance at eight transects in each of four land-use categories, representing different levels of forest degradation: old-growth forest, secondary forest, agroforest, and horticulture. While *Hyperolius molleri* was most abundant in secondary forest and horticulture, *Hyperolius thomensis* was almost exclusively found in agroforest. We interpret these differences based on reproductive traits, since both species deposit terrestrial eggs and have aquatic larvae, but reproduce in different microhabitats. *H. molleri* utilizes open water bodies bordered by vegetation for calling and oviposition, which human disturbance has made available in secondary forest and horticulture. In contrast, *H. thomensis* breeds in water-filled tree holes (phytotelmata), which predominantly occurred in agroforest, often within coral trees (*Erythrina* spp.). This first study on Santomean amphibian abundances revealed that *H. molleri* and *H. thomensis* males exhibit distinct nonlinear responses to forest degradation and may reap some benefit from human habitat alteration. However, despite their apparent tolerance to some anthropogenic disturbance, further land-use intensification may reduce overall habitat suitability for these and other endemic species.

Keywords

tropical montane forest, human-modified landscapes, coffee shade plantations, arboreal breeders, model averaging, Gulf of Guinea

Introduction

The current global rate of biodiversity loss is strongly connected to human activity (Ceballos et al., 2015; Newbold et al., 2015), as indicated by the geographic overlap of large human populations and high numbers of threatened species (Cincotta, Wisnewski, & Engelman, 2000; Luck, 2007). Many biodiversity hotspots coincide with populous and impoverished regions (Cincotta et al., 2000; Fisher & Christopher, 2007), mostly located in the tropics (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Here, land-use change is the key driver of terrestrial biodiversity decline (Sala, 2000). As a result of increasing human exploitation, tropical forests are being degraded and lost at accelerated rates (Kim, Sexton, & Townshend, 2015; Lewis, Edwards, & Galbraith, 2015). This poses a serious threat to ecosystem functioning

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(Foley et al., 2005) and the survival of roughly half of the world's terrestrial biodiversity (Groombridge & Jenkins, 2002).

Many studies on the effects of forest degradation have been dedicated to birds and mammals; far less to the Earth's most threatened group of terrestrial vertebrates: amphibians (Gardner, Barlow, & Peres, 2007; Stuart et al., 2004; Wake & Vredenburg, 2008). The global amphibian extinction crisis has been attributed to multiple factors (Beebee & Griffiths, 2005; Collins & Storfer, 2003; Hof, Araújo, Jetz, & Rahbek, 2011; Navas & Otani, 2007; Wake & Vredenburg, 2008). Land-use conversion is one of the greatest threats and has been known to impact amphibian populations (Beebee & Griffiths, 2005; Collins & Storfer, 2003; Hof et al., 2011). However, it remains unclear how individual species respond to human-modified habitats in the tropics (Barlow et al., 2007; Herrera-Montes & Brokaw, 2010; Wanger et al., 2009). Data on amphibian responses to land-use changes in tropical ecosystems are particularly scarce for most regions and species (Collen et al., 2009; Gardner, Fitzherbert, Drewes, Howell, & Caro, 2007). This is worrying as a growing body of evidence suggests that species-specific approaches are necessary to judge the effects of land use (Cushman, 2006; Nowakowski, Thompson, Donnelly, & Todd, 2017). Complex life histories, strong site fidelity, limited dispersal ability, ectothermy, semipermeable skin, and egg capsules make amphibians particularly sensitive to human-induced environmental changes (Blaustein & Bancroft, 2007; Navas & Otani, 2007). In particular, species with small geographical ranges and with either unstable or unknown population trends are highly susceptible to habitat modification (Nowakowski et al., 2017).

São Tomé and Príncipe is an African small island nation, facing severe rates of forest degradation and deforestation. Forest resources, including timber, medicinal plants, and bushmeat, constitute an essential part of the inhabitants' livelihoods (Carvalho, Rego, Palmeirim, & Fa, 2015; de Madureira, 2012; Ministry of Infrastructure, Natural Resources and Environment, 2016; Oyono et al., 2014; Salgueiro & Carvalho, 2002). São Tomé, one of the two main islands, is densely populated and the conservation of its endemic-rich natural ecosystems is in strong competition with crop production. However, protecting the biodiversity should be an urgent task (Wilkie, Eckelmann, Laverdiere, & Mathias, 2002), as island species are particularly prone to extinction due to their small population sizes (R. G. Gillespie, 2007). Declining biodiversity may reduce ecological function on islands, potentially impairing ecosystem processes (Cox & Elmqvist, 2000).

The amphibian fauna of São Tomé is composed by five species, all of which are endemic to the island (International Union for Conservation of Nature, 2016), that is, four frogs: *Hyperolius molleri* (Bedriaga, 1892), *Hyperolius thomensis* Bocage, 1886 (both Hyperoliidae), *Phrynobatrachus leveleve* Uyeda, Drewes, and Zimkus, 2007 (Phrynobatrachidae), *Ptychadena newtoni* (Bocage, 1886) (Ptychadenidae); and one caecilian: *Schistometopum thomense* (Bocage, 1873) (Dermophiidae). The two *Hyperolius* are arboreal, *Phrynobatrachus* and *Ptychadena* are ground dwellers, and *Schistometopum* is fossorial. With most studies having focused on the taxonomy of these species (Drewes, 2008), there is little scientific evidence on how they might be affected by land-use change. We focused here on *Hyperolius* spp. since arboreal species have been recently suggested to be more sensitive indicators to changes in forest structure than terrestrial species (Whitworth, Villacampa, Serrano Rojas, Downie, & MacLeod, 2017; but compare Ernst & Rödel, 2005, 2008). In addition, all other amphibian species were either extremely rare or absent on our study sites. *H. molleri* reproduces on leaves over stagnant or slow-moving water, whereas *H. thomensis* breeds in water-filled tree holes (Drewes & Stoelting, 2004). São Tomé offers a diverse array of land-use types (Dallimer, Parnell, Bicknell, & Melo, 2012; de Lima, Dallimer, Atkinson, & Barlow, 2013), including well-preserved native forests that can be used as a valuable baseline for the original state of the island (Jones, 1994). Old-growth forest (OF), secondary forest (SF), and agroforest (AF) each comprise around 30% of the island's surface (Salgueiro & Carvalho, 2002). Due to its limited accessibility, the OF of the higher elevations is among the best preserved on São Tomé (Oyono et al., 2014; Salgueiro & Carvalho, 2002). SFs, being mostly abandoned plantations, form a buffer zone around this OF (de Lima et al., 2013). Both forest types are currently under pressure from agricultural expansion and forest extraction activities, such as logging (Ministry of Infrastructure, Natural Resources and Environment, 2016), despite partly being within the São Tomé Obô Natural Park (Salgueiro & Carvalho, 2002). The region's special climatic conditions favor agricultural production. Most of São Tomé's coffee, one of its key export commodities (Central Intelligence Agency, 2014), is cultivated in the study region. Scattered in-between are horticultural fields (de Lima et al., 2013), used by small-scale farmers to provide vegetables for the internal market (Jones, Burlison, & Tye, 1991). Despite the lack of recent forest inventories, land-use practices are currently assumed to have intensified (de Lima et al., 2013; Oyono et al., 2014).

Tropical amphibian studies rarely cover extensive transitions from OF to deforested land (Gardner, Barlow, et al., 2007) or are based on species richness data only. However, abundance may be a more sensitive measure to compare differences between land-use types in the short term (Collen et al., 2009; Luck, Daily, & Ehrlich, 2003; Schneider-Maunoury et al., 2016). In this study, we aimed to examine the effects of different levels of forest degradation on São Tomé's amphibian abundance. Specifically, the following research questions were explored: (a) How do species abundances change along four different levels of forest degradation? and (b) Can environmental parameters explain this change? We hypothesized that OF, as the original cover of the island, is the main and most important habitat for its amphibian populations.

Methods

Study Area

The 857 km^2 oceanic island of São Tomé is part of the Cameroon Volcanic Line (Déruelle et al., 1991; Henriques & Neto, 2015) located approximately 250 km off the Gabonese coast, slightly north of the equator (Figure 1). São Tomé was discovered in 1470 by Portuguese navigators. Then, the island had no permanent settlement (Figueiredo, Paiva, Stevart, Oliveira, & Smith, 2011) and was almost entirely covered with lowland (<800 m asl), montane (800–1,400 m asl), and mist (>1,400 m asl) forest (Monod, 1960). Large clearings were subsequently made, especially during the 19th century, when almost all forests up to 1,500 m asl were cut to plant export and subsistence crops (Figueiredo et al., 2011; Juste & Fa, 1994).

São Tomé has an oceanic equatorial climate, but owing to the moist southwest winds and high mountains, it covers distinct climatic zones (Jones et al., 1991; Juste & Fa, 1994). Our study area was located in the montane forest zone (between 800 and 1,300 m asl, Figure 1). The annual mean temperature at Monte Café (690 m asl), the nearest large settlement, is 20.5°C, with a mean annual maximum temperature of 24.7°C and a mean annual minimum temperature of 16.5°C. The local absolute minimum temperature is 8.7°C (Brühl, 1993). The annual precipitation exceeds 2,000 mm, and the dry seasons are not very pronounced at this elevation, with rain falling throughout the year, in varying amounts (Jones et al., 1991).

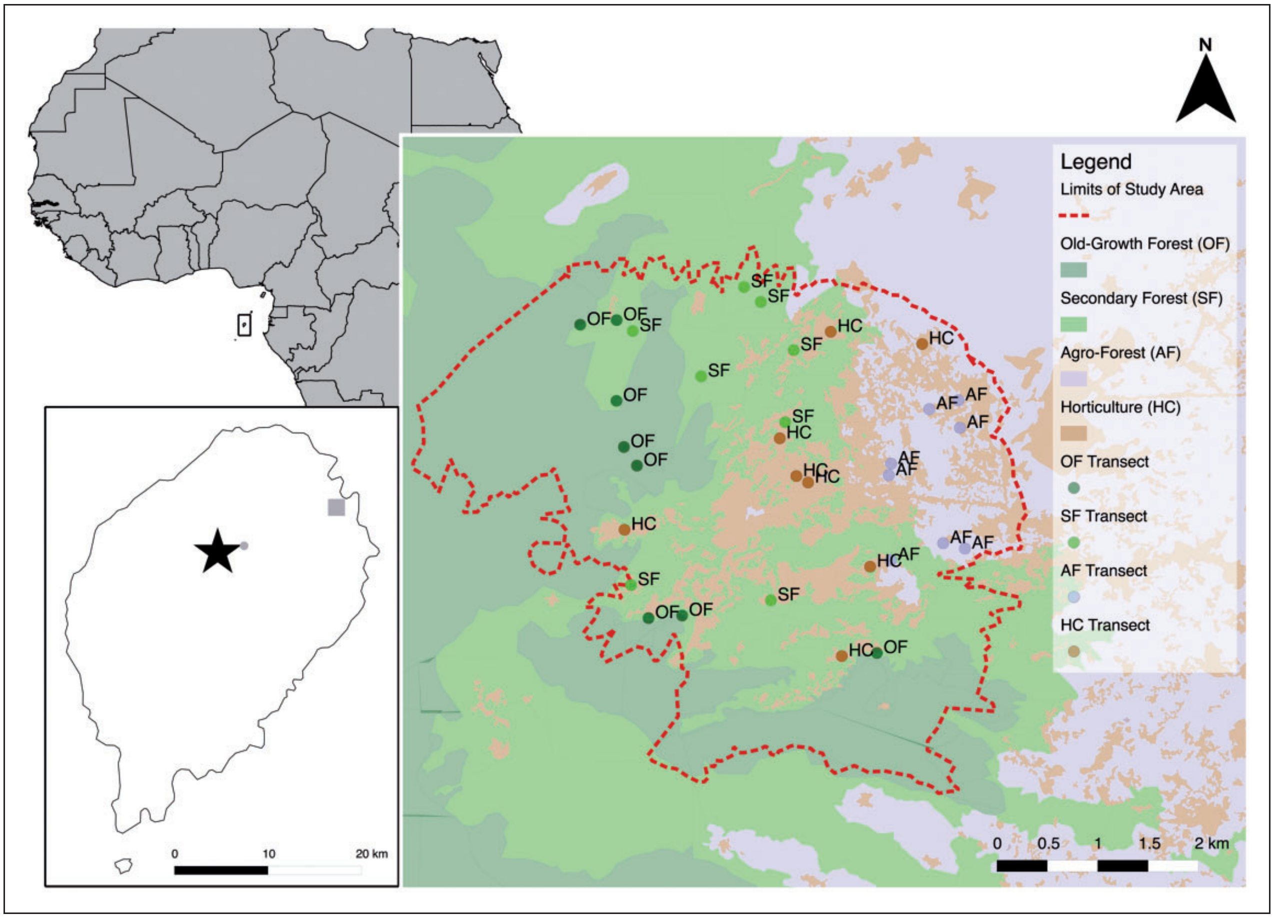

Figure 1. Different land-use types and location of transects within the study area. The inset in the top left shows the geographic location of São Tomé Island (black square) in the Gulf of Guinea. The inset in the bottom left shows the location of the study area (black star) on São Tomé Island. The gray dot indicates Monte Café, the nearest large settlement, and the gray square the capital of São Tomé.

Sampling Design

Land-use type classification. We considered four main land-use types ranging from OF to horticulture (HC; Salgueiro & Carvalho, 2002). OF includes areas with little human influence, mostly covered by dense, tall vegetation, and large trees, where native species predominate (Figueiredo et al., 2011; Salgueiro & Carvalho, 2002). SF results from agricultural abandonment or intensive logging and includes regenerating areas with high proportions of introduced species and few large trees (de Lima et al., 2013). AF is a multistrata management system in which high-canopy trees shade understorey agricultural plants (Salgueiro & Carvalho, 2002; Tscharntke et al., 2011). In the study area, these were perennial coffee plants, typically *Coffea arabica*, growing under the canopy of introduced, fast-growing species, such as coral trees (*Erythrina* spp.). The plantations are often intercropped with banana (*Musa* spp.) and taro (*Colocasia esculenta*; de Lima et al., 2013). HC was the only land-use type without a continuous tree cover but comprised solitary trees. This land-use type included annual and perennial crops such as cabbage (*Brassica oleracea*), bean (*Phaseolus vulgaris*), tomato (*Lycopersicon esculentum*), banana, cassava (*Manihot esculenta*), and taro (*Xanthosoma sagittifolium*; Jones et al., 1991; Ministry of Infrastructure, Natural Resources and Environment, 2016; Salgueiro & Carvalho, 2002).

Transect selection. Since there are no reliable land-use maps for São Tomé (de Lima et al., 2013), we used our knowledge of the region and Google Earth images (Google Inc., 2016) to classify land-use types in the study area. We then generated eight random points within each land-use category using QGIS (QGIS Development Team, 2016). The random points were identified in the field with the help of a GPS device (Garmin GPSmap 62s) and served as the localities for linear transects (cf. e.g., Doan, 2003; Pearman, Velasco, & López, 1995; Rödel & Ernst, 2004). Transect length was set to 100 m to ensure that transects did not cover more than one land-use type. The direction of each transect was chosen to assure that the terrain was accessible (i.e., not following a steep slope). The resulting 32 transects, eight in each land-use type (Figure 1), assured easy comparability of amphibian abundances across the land-use categories (Hirzel & Guisan, 2002). Open water bodies of any kind were absent from one SF and five AF transects. The average linear distance between transects was 315 m (range: 765 m). All 32 transects were located inside a base area of approximately 4 × 4 km. However, the surface of the study area was considerably larger due to the rugged terrain with altitudinal differences of over 500 m.

Data Collection

Habitat parameters. Prior to amphibian sampling, relevant environmental variables were recorded for all transects (Appendix A). To evaluate canopy openness, we took five hemispherical photographs on each transect; one every 25 m using a camera equipped with a fish-eye lens (Soligor DHG 0.19 × Fish Eye for Digital Ø 37 mm Japan), held vertically at eye level. We applied ImageJ (Schneider, Rasband, & Eliceiri, 2012) to split the red, green, and blue components of each photograph. The blue channel images were then converted into binary images. This conversion was automatic, except for a few cases, when suboptimal light exposure demanded manual thresholding. The percentage of open canopy for each image was obtained employing Gap Fraction Analysis (Gonsamo, Walter, & Pellikka, 2011). We then calculated the mean of the five pictures for each transect: 0% represented a completely closed canopy and at 100% no vegetation obscured the sky. We further recorded vegetation density for each transect as a whole in three different strata: canopy (height: > 20 m), lower tree (height: 3–10 m), and bush and shrub stratum (height: 0.5–1.5 m; Rödel & Ernst, 2004). For each stratum, we applied the following categories by eye: stratum absent, stratum reduced to single trees, stratum present but gaps predominating, stratum present with closed areas predominating, and stratum closed. We further counted all small trees (diameter at breast height, dbh, between 21 and 50 cm) and large trees (dbh larger than 50 cm) within 10 m to each side of the transect. In the same area, we documented presence of plant species or genera, including trees, shrubs, and herbs. To assess the availability of potential amphibian oviposition sites, we counted all tree holes visible in the same area up to 10 m aboveground. We also registered the presence of both stagnant and flowing open water bodies (irrespective of water-filled tree holes), including rain barrels, ponds, puddles, ditches, streams, and rivers, within a distance of 150 m from the transect. In one case in which two transects were only 130 m apart, the water bodies were assigned to the nearest transect. Following Rödel & Ernst (2004), we classified soil into four rough substrate types: forest soil, arenaceous humus soil, loamy soil, and arenaceous soil. We deployed one automatic thermologger per transect (Thermochron® iButtons© DS 1921G; accuracy ± 0.5°C, Maxim Integrated, San Jose, USA) to measure air temperature every hour for 30 days (December 30, 2014, to January 28, 2015). These devices were placed at ground level in the shade. From the data obtained, we extracted average, minimum, and maximum air temperature for each day (24 values), which were then averaged per transect over the 30-day period. The elevation was recorded every 25 m for each transect using the GPS from which the mean elevation of the respective transect was calculated.

Treefrog sampling. We performed amphibian counts from mid-December 2014 until the end of January 2015, 30 sampling nights in total. We visited each transect three times, which resulted in 96 transect walks (3 × 32 transects). The transects were surveyed between 5.45 and 8.45 pm at slow pace and constant speed. On average, sampling time per transect walk was 12 min. The order of transect visits followed a predefined random sequence. On all transect walks, we identified every individual detected visually and acoustically (breeding males), following AmphibiaWeb (2017); Drewes and Stoelting (2004); Schiøtz (1999); and Uyeda, Drewes, and Zimkus (2007). Calling males were recorded up to 30 m to each side of the transect. We considered a minimum number of individuals by allocating repeated calls of the same direction and distance to a single individual. *H. molleri* emits a series of ''clack'' sounds, whereas the advertisement call of *H. thomensis* consists of a creaking buzz of lower frequency (Schiøtz, 1999). The two *Hyperolius* species have been reported to use calling positions at different heights, that is, *H. molleri* at 0.3 to 1 m and *H. thomensis* at 5 m aboveground (Fahr, 1993). Visual detections included sightings on the ground and in trees along a band of 2 m on each side of the transect. Species identity, developmental stage (i.e., egg, tadpole, juvenile, or adult), and, if possible, sex were recorded for all detected specimens. We counted egg clutches but not egg numbers within clutches. *H. molleri* and *H. thomensis* are known to hybridize in the study area (Bell, Drewes, & Zamudio, 2015). Potential hybrids were only seen in the broader study region. Sightings and calls (cf. Gilbert & Bell, 2018) of all individuals on transects could unambiguously be assigned to one of the two species.

Data Analyses

Our aim was to determine how species' abundances change along different types of forest degradation and which environmental variables best explain this change. Hence, we applied two steps of analysis, for which all species-individuals per transect were summed up over the whole collection period. Abundance data were zero-inflated and not normally distributed.

First, we compared the abundances of each amphibian species between land-use types using Kruskal–Wallis rank sum tests followed by individual pairwise Wilcoxon rank sum tests. We calculated indicator values (IndVals) for each species in all land-use categories (function indval, library labdsv), based on their habitat specificity and fidelity, which range between 0% (no indication) and 100% (excellent indication). The index reaches its maximum when a species only occurs in one land-use category (high specificity) and is present at all sample sites of that land-use category (high fidelity; Dufrêne & Legendre, 1997). A species that has a high IndVal (usually more than 70%) is considered a character species. Species that show medium specificity and medium fidelity are much better indicators of environmental change and are known as detector species (da Mata, McGeoch, & Tidon, 2008; McGeoch, van Rensburg, & Botes, 2002).

Second, we applied model averaging to identify the environmental variables that best explained the abundance of each species. To lower the collinearity, we reduced the number of predictor variables based on Kruskal–Wallis rank sum tests, scatterplots, and variance inflation factors (≤ 3; Zuur, Ieno, & Elphick, 2010). We standardized all continuous predictor variables between 0 and 1 by subtracting the minimum value and dividing by the maximum value to avoid having comparatively large values distort the results. To rule out systematic biases, we checked the abundance data for temporal autocorrelation by plotting autocorrelation functions (ACFs). No dependence was revealed regarding the timing of observation (Appendix B). However, significant spatial autocorrelation, a frequent problem in ecological data (Hawkins, 2012), was detected using Monte Carlo simulation of Moran's I (*H. molleri:* $p = .0002$; *H. thomensis:* $p = .0000$). Model averaging based on Akaike weights across spatial autoregressive (SAR) models is a robust method to address this issue (Diniz-Filho, Rangel, & Bini, 2008). We thus chose spatial simultaneous autoregressive lag model estimation and employed the function "lagsarlm" (library spdep) to define a global model (Bivand & Piras, 2015). All possible combinations of the independent predictor variables were fitted using the function "dredge" (library MuMIn) on the global model (Bartón, 2016). To identify key predictor variables, model averaging was carried out with the function "model.avg" (library MuMIn) for a 95% confidence model set, resulting in estimates, standard errors, and relative variable importance.

All statistical analyses were performed in R, Version 3.0.0 (R Core Team, 2013). Additional packages used included MASS (Venables & Ripley, 2002) and vegan (Oksanen et al., 2015). Land-use categorization coincided mostly with differences in canopy density or openness, plant species composition, and substrate type as confirmed by Kruskal–Wallis rank sum tests (p values $< .0003$). We also conducted a one-way analysis of similarities (ANOSIM) on the plant species data (Appendix C) to validate the land-use type categorization (Clarke, 1993).

Results

During the transect walks, we acoustically documented 72 *H. molleri* and 26 *H. thomensis* individuals. Visual data were only obtained for one adult and nine clutches of *H. molleri* and was therefore not further considered. Neither visual nor acoustic evidence was found for *Hyperolius* hybrids within transects. As expected, we encountered two additional amphibian species in the study area; however, *S. thomense* was observed only twice along transects and *P. leveleve* exclusively off transect.

The two *Hyperolius* species differed in their abundances across the four land-use types according to the Kruskal–Wallis rank sum (*H. molleri:* $p = .0079$; *H. thomensis:* $p = .000$) and the pairwise Wilcoxon rank sum tests (Table 1). However, *H. molleri* abundances were only significantly different between AF (1 individual) and SF (33 individuals). The latter was closely followed by HC (32 individuals) and OF (6 individuals). The abundance of *H. thomensis* in AF (23 individuals) was significantly different from those in all other land-use types (three individuals in SF and none in OF or HC). *H. molleri* reached the highest IndVals in SF (40%) and HC (28%; Table 2). Overall, it had a low indicator potential, as it was not restricted to one land-use type and only occurred at some transects of each land-use type. Contrarily, *H. thomensis* was a character species showing an extraordinary specificity and fidelity to AF (IndVal: 88%; Table 2).

For our global SAR models, land-use type, lower tree density, bush and shrub density, number of small trees, number of large trees, number of tree holes, water body availability, and maximum air temperature were kept as independent predictor variables. Model-averaged results for *H. molleri* and *H. thomensis* only included those variables that were part of the respective 95% confidence model set. Model averaging for the abundance of *H. molleri* revealed highest relative importance of the variables land-use type and water body availability (Table 3). The highest *H. molleri* abundances were reached in SF and HC. No frogs were observed when open water bodies were absent (Figure 2). Model averaging for *H. thomensis* resulted in highest relative importance of water body availability, number of tree holes, and land-use type (Table 3). Few *H. thomensis* individuals were found in the presence of open water bodies, but the number of tree holes was positively correlated with *H. thomensis* abundances. *H. thomensis* was considerably more abundant in AF than in any of the other three categories (Figure 2). Most tree holes were found in AF (15), while few were recorded for SF (5) and OF (1), and none for HC. Sixteen of the 21 tree holes occurred in trees of the nonnative genus *Erythrina*.

Table 1. Pairwise Wilcoxon Rank Sum Tests on Differences in *Hyperolius* Abundances Between Land-Use Types.

Species		OF	SF	AF	HC
Hyperolius molleri	OF				
	SF	.104			
	AF	.364	**.017**		
	HC	.364	.873	.119	
Hyperolius thomensis	OF				
	SF	.342			
	AF	**.002**	**.005**		
	HC		.342	**.002**	

Note. $n = 8$ for each land-use type. Results described through p values; significant p values ($<.05$) marked in boldface. OF = old-growth forest; SF = secondary forest; AF = agroforest; HC = horticulture.

Table 2. Indicator Values (IndVals) of *Hyperolius* spp. According to Land-Use Types.

Species	OF	SF	AF	HC
Hyperolius molleri	4	40	0	28
Hyperolius thomensis	0	3	88	0

Note. $n = 8$ for each land-use type. OF = old-growth forest; SF = secondary forest; AF = agroforest; HC = horticulture, given as percentages with 0% meaning no indication (species not present in the respective land-use type) and 100% meaning excellent indication (species present at all transects of the respective land-use type and absent from all other land-use types).

Discussion

Our amphibian data contribute to understanding the responses of arboreal frog species to tropical land use. Amphibian studies measuring abundances commonly show conflicting outcomes with regard to land-use change. Many studies using species richness reveal declines toward disturbed areas (Gardner, Fitzherbert, et al., 2007; Hillers, Veith, & Rödel, 2008; Pineda, Moreno, Escobar, & Halffter, 2005; Wanger et al., 2010), presumably owing to lower structural complexity (Gardner, Barlow, et al., 2007) or altered microclimate (Hillers et al., 2008). However, inconsistencies among results of any measure hamper the search for cross-species generalities. The underlying cause may be species-specific sensitivities to habitat modification and associated traits (Nowakowski et al., 2017). We try to shed light on the link between landscape variables and reproductive traits in *Hyperolius* spp., advocating for species-centered approaches (Becker, Loyola, Haddad, & Zamudio, 2010; Betts et al., 2014).

Treefrog Species Response to Land-Use Intensification

São Tomé's endemic treefrogs showed species-specific complex nonlinear responses to the different levels of forest degradation. *H. molleri* has been considered a generalist that can adapt to modified landscapes (International Union for Conservation of Nature, 2016), occurring in primary forest, SF, and coffee plantations and using water reservoirs within agricultural sites (Bell et al., 2015). We confirmed its presence in all of these land-use types but in distinctly different abundances. The species was, however, most numerous in SF, as indicated by Fahr (1993) and Drewes and Stoelting (2004). *H. thomensis*, in contrast, was almost exclusively restricted to AF, with a few records in SF. This suggests that this species tolerates intermediate

Table 3. Summary Results Obtained After Model Averaging (Natural Average: Non-shrinkage).

Species	Variable	Estimate	Standard error	Relative variable importance
Hyperolius molleri	(Intercept)	0.092	1.376	
	Land-use type 2[a]	2.852	1.194	0.68
	Land-use type 3	−0.275	1.584	0.68
	Land-use type 4	2.796	1.294	0.68
	Water body presence[b]	2.277	1.202	0.50
	Maximum air temperature	−8.941	10.735	0.21
	Number of small trees	−1.643	1.839	0.20
	Number of tree holes	1.198	1.584	0.20
	Number of large trees	−0.876	2.392	0.18
	Bush and shrub density 2[c]	0.367	1.541	<0.01
	Bush and shrub density 3	0.814	1.140	<0.01
	Bush and shrub density 4	−1.062	1.318	<0.01
Hyperolius thomensis	(Intercept)	1.594	0.434	
	Water body presence[b]	−1.552	0.401	1.00
	Number of tree holes	1.295	0.390	0.94
	Land-use type 2[a]	0.043	0.276	0.31
	Land-use type 3	1.282	0.506	0.31
	Land-use type 4	−0.020	0.283	0.31
	Number of small trees	−0.507	0.413	0.26
	Number of large trees	−0.356	0.495	0.19
	Maximum air temperature	0.381	2.325	0.15

Note. Effects of each variable on *Hyperolius* abundances on transects, including estimates, standard errors, and relative variable importance (land-use type 2: secondary forest, land-use type 3: agroforest, land-use type 4: horticulture; bush and shrub density 2: reduced to single trees, bush and shrub density 3: gaps predominating, bush and shrub density 4: closed areas predominating).

[a] Land-use type 1 (old-growth forest) was the reference category. [b] Water body absence was the reference category. [c] Bush and shrub density 1 (absent) was the reference category.

levels of forest degradation and may benefit from human-induced increased availability of tree holes. This finding contradicts previous data, assuming the species to be an OF specialist (Drewes & Stoelting, 2004), as we did not find it in this land-use type. However, the apparent absence of *H. thomensis* from our OF transects might be due to its overall low abundance.

Species-Specific Habitat Associations

Since *H. molleri* tadpoles develop in stagnant or slow-flowing water, the species' association with the presence of open water bodies was not surprising. We could not determine any preference with regard to stagnant versus flowing. So far it is not known whether tadpoles of this species develop equally in different water body types. Water bodies were overall more common in SF, HC, and OF than in AF, where the deep-rooted plantation systems do not require artificial watering. Regarding microstructures, SF appeared to offer the ideal combination for the development of *H. molleri* offspring, namely, puddles on roads and numerous streams framed by overhanging vegetation. *H. molleri* requires vegetation with large, stable leaves overhanging water to deposit clutches (Drewes & Stoelting, 2004). Likewise, HC frequently provided adequate man-made reproduction sites such as irrigation ponds and rain barrels. Here, the walls of the water bodies functionally replaced overhanging vegetation as clutch oviposition sites. Man-made water sources in tropical farmland have been suggested to be crucial for amphibian biodiversity as natural ecosystems become scarcer (Mendenhall et al., 2014). OF, mostly located on steep slopes, harbored only few streams or rivers, usually with high-velocity flows. These habitats are likely unsuitable for *Hyperolius* larvae, which usually have no morphological adaptations for fast flowing streams (Channing, Rödel, & Channing, 2012; Drewes & Stoelting, 2004; International Union for Conservation of Nature, 2016). The higher abundances of *H. molleri* in SF and HC may thus be explained by its breeding requirements, since both land-use types provide a suitable combination of vegetation or man-made structures and open water bodies. We frequently spotted clutches of *H. molleri* on transects with considerable vegetation gaps, which

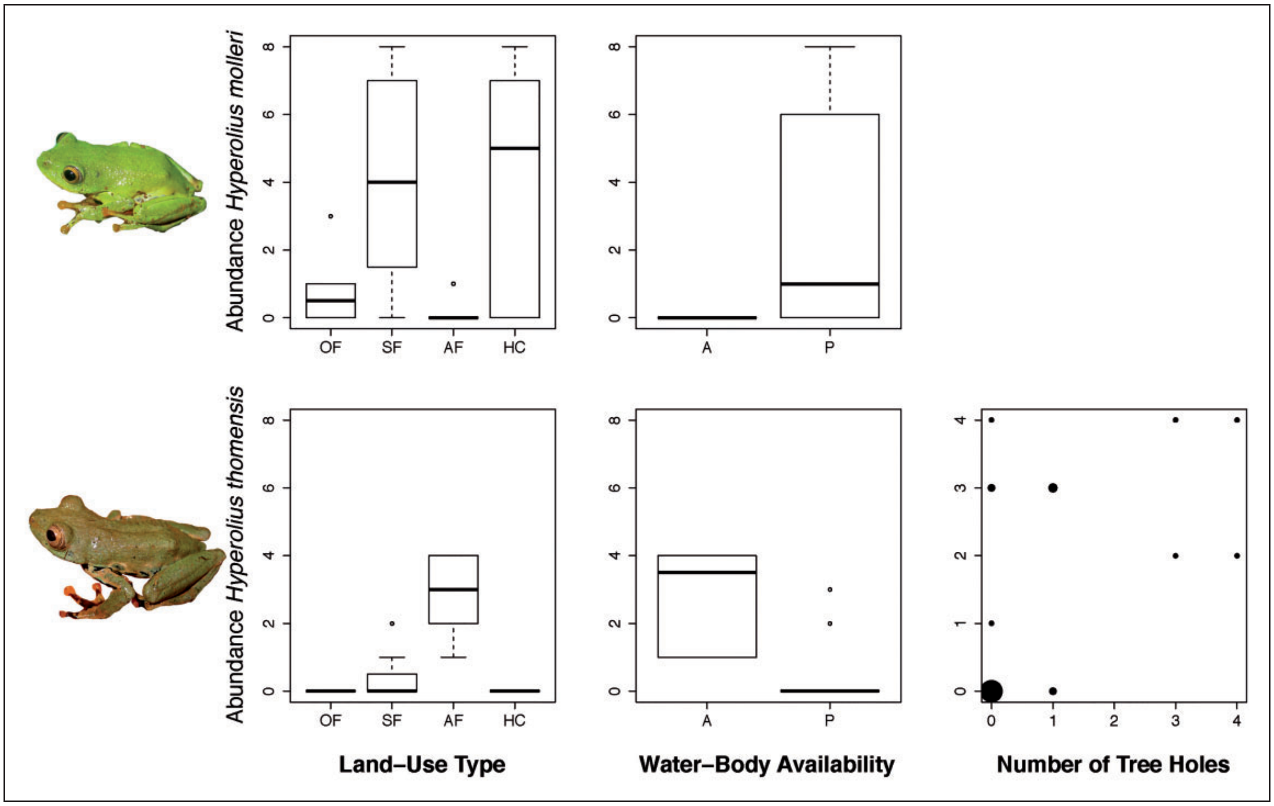

Figure 2. Relationship between *Hyperolius* abundances and variables with the highest relative variable importance values (>30; Table 3): Land-use type (*H. molleri* and *H. thomensis*; $n = 8$ for each land-use type), water body availability (*H. molleri* and *H. thomensis*), and number of tree holes (*H. thomensis*). Box and whisker values refer to median, interquartile range, minimum and maximum, and extreme values. OF = old-growth forest; SF = secondary forest; AF = agroforest; HC = horticulture; A = absence of water; P = presence of water.

suggests that it might also require the specific microclimatic conditions best found in SF and HC. In the study area, and elsewhere, increased disturbance correlated with greater canopy openness and increased ambient temperature (Halverson, Skelly, Kiesecker, & Freidenburg, 2003).

The habitat preferences of *H. thomensis* also reflect a compromise between water availability and vegetation structure, linked to breeding ecology. The species likewise deposits its eggs outside of water and has aquatic larvae. By contrast, it heavily depends on the availability of water-filled tree holes which serve as breeding sites (Drewes & Stoelting, 2004). The species was clearly more abundant in AF, since the fast-growing shade trees, including *Erythrina* spp., tend to form cavities (Ishiguri et al., 2007). These nitrogen-fixing shade tree species do not naturally occur in OF (Lejoly, 2000). OF and SF mostly host native, slow-growing trees, and in HC, only few trees are present; both factors likely account for lower phytotelmata availability. The absence of aquatic habitats in forested environments may have led to the evolution of the phytotelmata-breeding strategy of *H. thomensis* and to its divergence from the *H. molleri* lineage (Bell et al., 2015). Our results even suggest that the absence of open water bodies favors the occurrence of *H. thomensis*; however, such a causal relationship seems unlikely.

Spatial behavior in amphibians is a trade-off between the need to find suitable microhabitats for reproduction (G. R. Gillespie, Lockie, Scroggie, & Iskandar, 2004; Refsnider & Janzen, 2010), thermoregulatory requirements (Magnuson, Crowder, & Medvick, 1979), and predator avoidance (Vredenburg, 2004). Females selecting oviposition sites search for a trade-off between these pressures (Thurman, Garcia, & Hoffman, 2014). Males may equally take them into account when calling to attract females (G. R. Gillespie et al., 2004; Rudolf & Rödel, 2005). The different responses of *H. molleri* and *H. thomensis* males to the shift in anthropogenic land use in our area seem mostly related to their differences in reproductive biology. To varying degrees, both species appear to profit from some anthropogenic disturbance. This may, however, only concern the breeding periods and life stages of these species. Other land-use types may be essential during the nonbreeding periods, with a possible negative effect of habitat degradation on survival rates (Becker, Fonseca, Haddad, & Prado, 2010; Pittman, Osbourn, & Semlitsch, 2014). In addition, connectivity and minimum size of land-use patches are likely to influence population viability (Becker, Fonseca, et al., 2010; Halpern, Gaines, & Warner, 2005). Overall, *H. molleri* may be better suited to survive major habitat changes than *H. thomensis*, since it is well adapted to the nonforested habitats found in intensive land-use areas. Hybrids, which are likely to be *H. molleri* carrying *H. thomensis* mitochondrial haplotypes (Bell et al., 2015), may deal similarly with land-use change depending on their breeding habitat. This raises the issue of whether *Hyperolius* hybrids contribute to conservation goals, such as the maintenance of ecological functions, or negatively affect the genetic fitness of the "pure" species (Jackiw, Mandil, & Hager, 2015).

Implications for Conservation

Despite the apparent tolerance of *H. molleri* and *H. thomensis* to some forest degradation, the importance of OF to overall biodiversity conservation remains unquestioned (Gibson et al., 2011). The richness and abundance of São Tomé's endemic bird species decrease toward more intensively used ecosystems, which highlights the irreplaceability of São Tomé's natural forests (de Lima et al., 2013). Different taxonomic groups and species within groups do not necessarily exhibit similar responses to forest degradation (Barlow et al., 2007; Wolters, Bengtsson, & Zaitsev, 2006). Thus, optimal conservation strategies will be species dependent. Further research including all amphibian species at any life cycle phase, and other taxonomic groups, as well as additional systems such as lowland forests, cocoa, and oil palm plantations would help clarify the island-wide impacts of land-use intensification.

São Tomé's human-modified landscapes currently show potential for the conservation of endemic amphibians. The ongoing intensification in all land-use types may, however, exacerbate in the future. The current trend of forest conversion to HC, palm oil plantations, and other unshaded cultivations (Oyono et al., 2014) may be further fueled by the explosive population growth and foreseeable increment of coffee, cocoa, palm oil, and coconut exports (United Nations, Department of Economic and Social Affairs, Population Division, 2017). Climate change is likely to contribute to a reduction in forested land by forcing small-scale farmers to move horticultural parcels to higher altitudes, where OF and SF currently predominate. While deforestation could primarily affect *H. thomensis* through the loss of tree habitats, any impact on *H. molleri* may be less direct but likewise urges caution. Concerted conservation strategies, taking life-history traits into account, are essential.

Appendices

Appendix A

Table A1. Environmental Parameters Assessed per Transect and Definition of Units/Categories and Their Scales.

Variable		Unit/Categories	Scale
Biotic	(1) Canopy openness	%	Continuous
	(2) Canopy density (height: > 20 m) (3) Lower tree density (height: 3–10 m) (4) Bush and shrub density (height: 0.5–1.5 m)	1: Absent 2: Reduced to single trees 3: Gaps predominating 4: Closed areas predominating 5: Closed	Categorical
	(5) Number of small trees (dbh: 21–50 cm) (6) Number of large trees (dbh: > 50 cm) (7) Number of tree holes	Natural number	Continuous
	(8) 75 plant species/genera	0: Absence of species 1: Presence of species	Categorical
Abiotic	(9) Water body availability	0: Absence of water 1: Presence of water	Categorical
	(10) Substrate type	1: Forest soil 2: Arenaceous humus soil 3: Loamy soil 4: Arenaceous soil	Categorical
	(11) Average air temperature (12) Minimum air temperature (13) Maximum air temperature	°C	Continuous
	(14) Altitude	M	Continuous

Appendix B

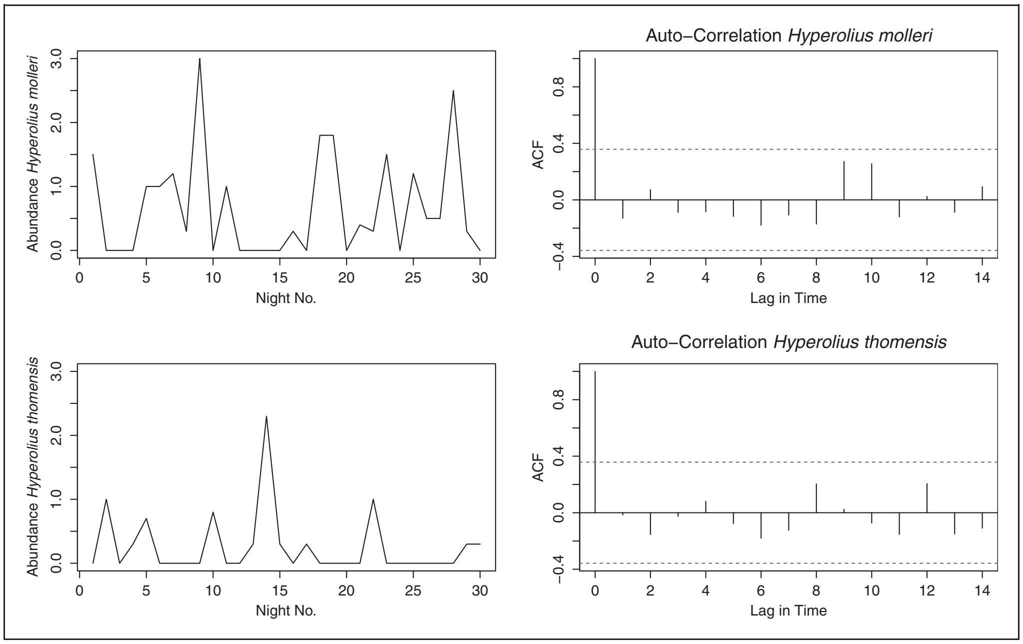

Figure B1. Temporal independence regarding the nights of observation: Abundances of *Hyperolius molleri* (top) and *H. thomensis* (bottom) were averaged over all transects visited per night and plotted against each night in graphs on the left and ACFs are given as R^2 values in graphs on the right (1 lag in time is equivalent to 2 nights). The ACF computes the Pearson correlation between the time series of frog abundance and the same series shifted by k lags in time. Subsequently, the estimated ACFs can be inferred from the graph at the different lags of time. Dashed lines therein represent 95% confident bands, which means any value exceeding these lines indicates a significant correlation. At Lag 0, the autocorrelation is by default 1 (Zuur et al., 2010).

Appendix C

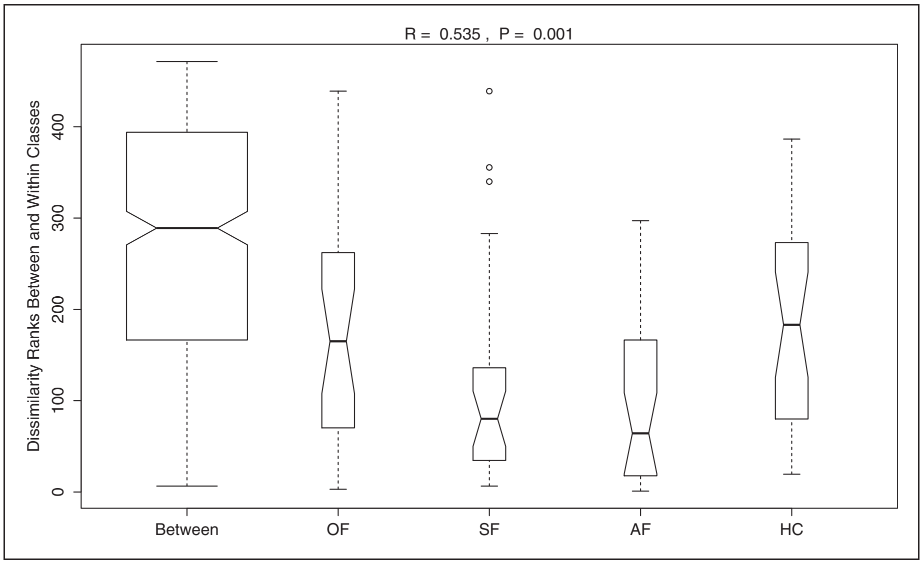

Figure C1. Validating the land-use type classification: ANOSIM of the plant communities with associated *r* value and *p* value. The range of dissimilarity ranks between and within land-use types is shown by boxplots; Between-boxplot: dissimilarity ranks between transects of different land-use groups ($n = 384$); OF-boxplot (old-growth forest)/SF-boxplot (secondary forest)/AF-boxplot (agroforest)/HC-boxplot (horticulture): Dissimilarity ranks between transects of each land-use group ($n = 28$). An *r* value close to 1 indicates high dissimilarities between groups, one close to 0 equal dissimilarities within and between groups, and one below 0 low dissimilarities between groups.

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